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Developmental expression patterns of *six6*: A gene linked with spawning ecotypes in Atlantic salmon

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ABSTRACT

The Atlantic salmon has been studied extensively, particularly as a model for understanding the genetic and environmental contributions to the evolution and development of life history traits. Expression pattern analysis *in situ*, however, is mostly lacking in salmon. We examine the embryonic developmental expression of *six6*, a candidate gene previously identified to be associated with spawning ecotypes and age at sexual maturity, in Atlantic salmon. *Six6* is a member of the sine oculis homeobox family of transcription factors and is known to regulate eye and brain development in other vertebrates. We assay the expression of this gene in embryonic Atlantic salmon *Salmo salar* by whole-mount *in situ* hybridization. In line with earlier studies in other vertebrate species, we find conserved expression in the developing brain and sensory organs, including optic and olfactory primordia. However, we also find previously unreported domains of expression that suggest additional roles in axial and appendicular development, cardiovascular, intestinal, and sensory organogenesis. Each of these systems are important in the sensory ecology of Atlantic salmon, suggesting it is plausible that *six6* may have pleiotropic roles in this complex phenotype.

1. Introduction

The Atlantic salmon (*Salmo salar* L.) is an exciting system for exploring the genetic variation that underlies the evolution of phenotypic diversity. Atlantic salmon have an anadromous life cycle whereby mature fish spawn in rivers and juveniles remain in the freshwater environment for 1–7 years, after which they migrate to sea for a varying number of years before returning to reproduce, often in their natal river. Some of the traits behind this complex life-history strategy include adaptation to the local environments of their spawning grounds, variation in age at maturity, and the ability to transform their physiology for marine and freshwater environments (reviewed in Jonsson and Jonsson, 2011).

Recent studies examining patterns of variation across the genome of salmonids identified several genome regions inferred to be under diversifying selection and/or linked with the abovementioned traits (Bourret et al., 2013; Moore et al., 2014; Barson et al., 2015; Lemay and Russello, 2015; Veale and Russello, 2017; Pritchard et al., 2018). One such locus, near the sine *oculis-related homeobox 6* (*six6*) gene on chromosome 9, has been found to associate with age at maturity (Johnston et al., 2014; Barson et al., 2015; Sinclair-Waters et al., 2020) and spawning ecotype in salmonids, including Atlantic salmon and sockeye salmon, *Oncorhynchus nerka*. More specifically, *six6* alleles have been associated with stream vs lake-shore spawning ecotypes in sockeye salmon (Veale and Russello, 2017) and seasonal return migration timing of Atlantic salmon sub-populations (Pritchard et al., 2018; Cauwelier et al., 2018). *SIX6* also associates with size and age at maturity in humans (Perry et al., 2014; Day et al., 2017) and is required for fertility and puberty in mice (Larder et al., 2011; Pandolfi et al., 2019). In Atlantic salmon, the chromosome 9 *six6* paralogue is expressed in the brain, eye, gill, and testis, and is hypothesized to contribute to maturation regulation via the brain-pituitary-gonadal axis (Kurko et al., 2020).

Six6 is a member of the sine oculis homeobox family of transcription

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factors that was first identified from a mutation in a gene called *sine oculis* in *Drosophila melanogaster* that affects the visual system (Cheyette et al., 1994; Serikaku and O'Tousa, 1994). *Six6* has evolutionary conserved roles in the control of eye development in fly, fish, frog, chick, and mouse (Seo et al., 1998; Toy et al., 1998; Jean et al., 1999; Lopez-Rios et al., 1999, 2003; Toy and Sundin, 1999; Zuber et al., 1999; Ghanbari et al., 2001; Ogawa et al., 2019). Two additional SIX family member genes are found in flies, *optix* and *DSix4*, and there are currently three subclasses of SIX proteins, each of which contain one fly gene and their orthologs: *Six1/2* (*sine oculis*), *Six3/6* (*optix*), and *Six4/5* (*DSix4*). *Optix* and its orthologs also regulate eye development, whereas *DSix4* and its orthologs function primarily in mesoderm derivatives (reviewed in Kumar 2009). SIX genes are broadly conserved in sequence and function, and frequently cooperate with other SIX genes to regulate organogenesis (Diacou et al., 2018; Garcez et al., 2014; Kawakami et al., 2000; Kobayashi et al., 2007; Ogawa et al., 2019). Despite the wealth of knowledge of expression patterns in the gene family, there is no information about specific expression domains in salmon. Given the gene's link with ecologically relevant phenotypes, this would be an important first step towards understanding the possible functional mechanisms resulting in such ecologically relevant variation.

Here, we examine the developmental expression of *six6* in Atlantic salmon embryos from approximately the eyed-egg stage of development through hatching using whole-mount *in situ* hybridization. Our data support a conserved role for this gene in the development of the cranial sensory organs, and suggest the evolution of novel expression in Atlantic salmon potentially related to spawning and migration.

2. Results

The common ancestor of salmonids underwent a salmonid-specific fourth vertebrate whole-genome duplication (WGD) (Macqueen and Johnston, 2014; Lien et al., 2016), and, consequently, there are four paralogues of *six6* in the Atlantic salmon genome on chromosomes 1, 7,

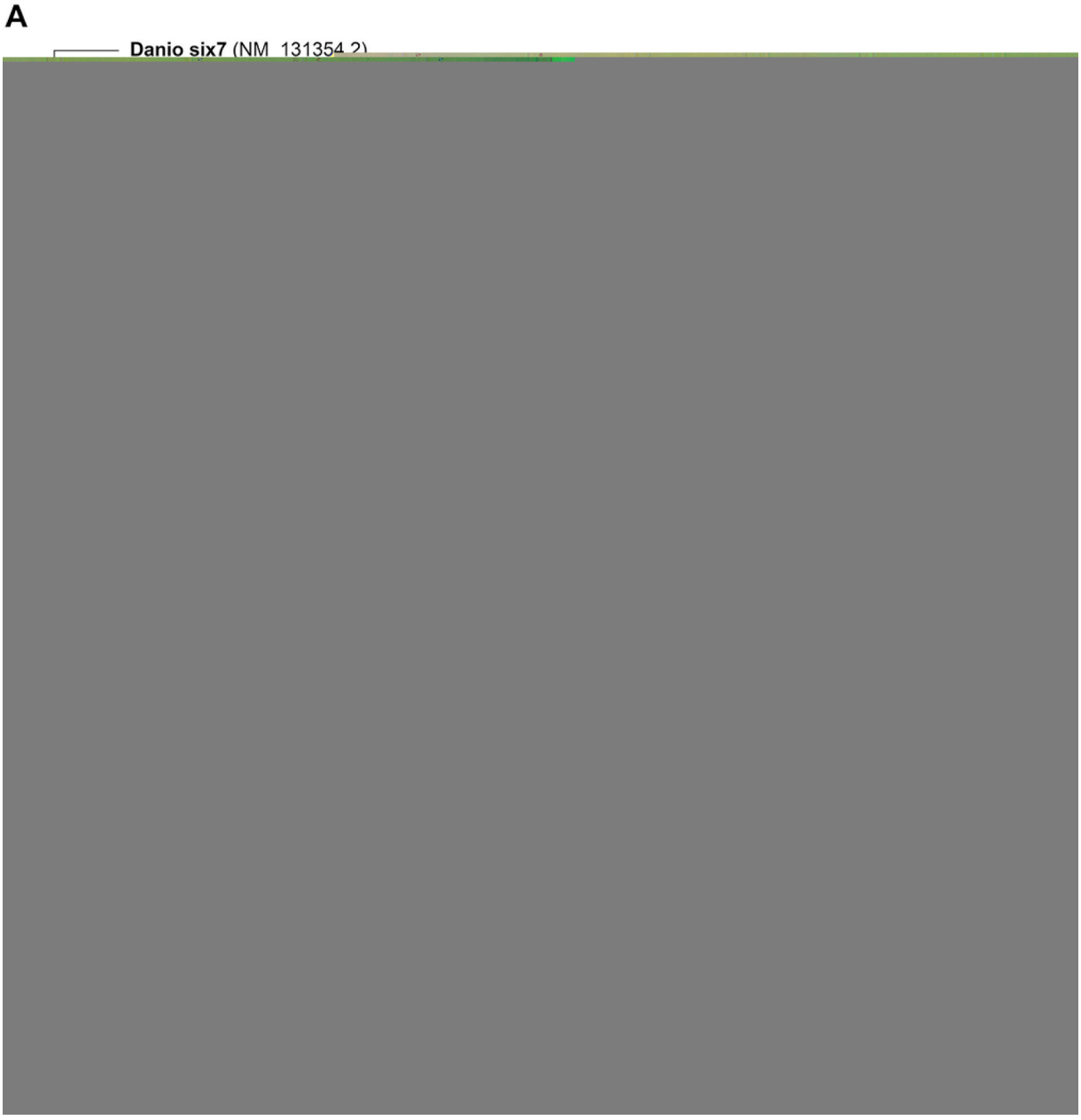

Fig. 1. **(A)** Maximum-likelihood tree of SIX3/6 nucleotide sequences. Accession numbers are bracketed after each paralogue. **(B)** Amino acid alignment of SIX3 and SIX6 paralogues. The SIX domain (top) and homeodomain (bottom) sequences of SIX proteins are highly conserved.

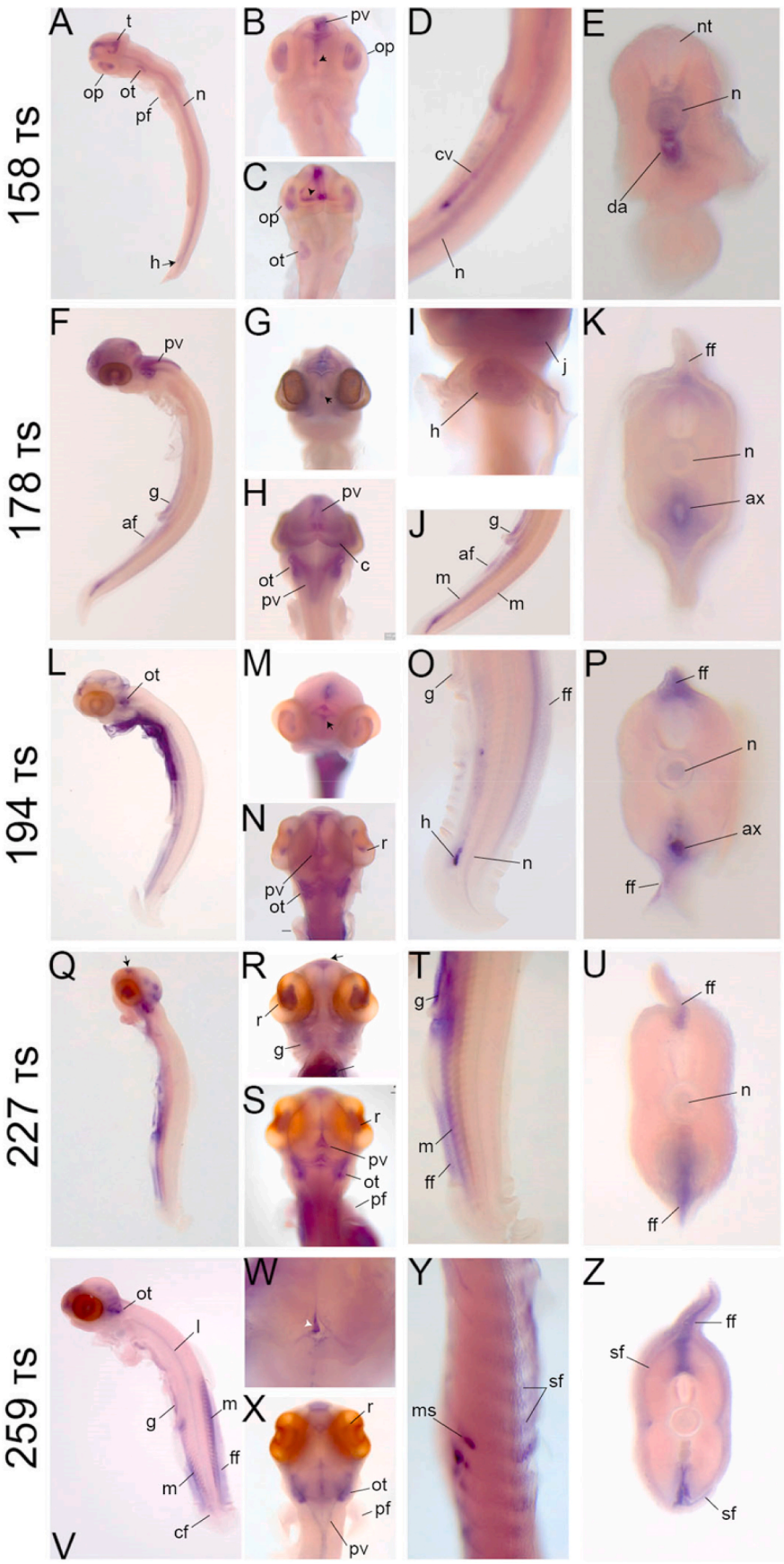

Fig. 2. Developmental expression of *six6* in Atlantic salmon embryos. **(A–E)** 158 τ_s embryos shown in lateral **(A, D)**, frontal **(B)**, and dorsal **(C)** view, and in section **(E)**. **(F–K)** 178 τ_s embryos shown in lateral **(F, J)**, frontal **(G, I)**, and dorsal **(H)** view, and in section **(K)**. **(L–P)** 194 τ_s embryos shown in lateral **(L, O)**, frontal **(M)**, and dorsal **(N)** view, and in section **(P)**. **(Q–U)** 227 τ_s embryos shown in lateral **(Q, T)**, frontal **(R)**, and dorsal **(S)** view, and in section **(U)**. **(V–Z)** 259 τ_s embryos shown in lateral **(V)**, dorsal **(W–X)**, and ventral **(Y)** view, and in section **(Z)**. af, anal fin; ax, axial vasculature; c, cerebellum; cf, caudal fin; cv, caudal vein; da, dorsal artery; ff, fin fold; g, gut; gi, gill; h, heart; he, hematopoetic; j, jaw; l, lateral line; m, myotome; ms, myosepta; n, notochord; nt, neural tube; ol, olfactory (black arrows); op, optic; ot, otic; p, pineal gland (white arrowhead); pf, pectoral fin; pv, periventricular tissue; r, retina; sf, slow muscle fibers; t, tectum (black arrowhead).

Author contributions

Jacqueline Moustakas-Verho: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Visualization, Writing - original draft, Writing - review & editing. Johanna Kurko: Conceptualization, Data curation, Investigation, Methodology, Writing - review & editing. Andrew House: Data curation, Investigation, Writing - review & editing. Jaakko Erkinaro: Resources. Paul Debes: Conceptualization, Data curation, Investigation, Methodology. Craig Primmer: Conceptualization, Data curation, Funding acquisition, Investigation, Resources, Writing - review & editing. All authors approved the manuscript.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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